BREEDING BEHAVIOR OF THE LOUISIANA HERON

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Information on the breeding behavior of the Louisiana Heron (*Hydranassa tricolor*) lacks sufficient detail to permit comparison with other ardeids. Both Bent (1926) and Palmer (1962) summarized the available data from the literature and drew upon previously unpublished information from contributors. Other studies (i.e., Teal 1965, Jenni 1969) deal with the reproductive success or ecology. I have described the displays characteristic of the breeding period (Rodgers 1977). This paper reports on the breeding behavior and nesting ecology of the Louisiana Heron.

STUDY AREA

Most fieldwork was carried out on Grand Island, Barataria Bay, Plaquemines Parish, Louisiana. Except for a few scattered oyster shell beaches, the island is covered by 5-20 cm of water during high tide, but drains almost completely at low tide except for a few inland pools. Predominant vegetation includes black mangrove (Avicennia nitida) and cordgrass (Spartina alterniflora).

Observations were made from blinds at 2 sites. Site A was characterized by tall, dense black mangrove averaging 1.5–2 m high with little or no open cordgrass areas. Site B was characterized by numerous small, low-lying clumps scattered throughout an equal area of cordgrass. Herons were designated as to which site they occupied, for example, male A1 or B1. Most herons and ibises fed in surrounding estuarine regions of Barataria Bay. Hence, Grand Island was used by the Louisiana Heron primarily as a breeding site, though also used for roosting at other times of the year.

PLUMAGE CHANGES

Palmer (1962) described the nuptial molt in preparation for breeding by the Louisiana Heron. The soft-part color depicted in a colorplate (page 367) that accompanies the description requires some revision for the Louisiana Heron on the coast of Louisiana.

During the courtship phase of the breeding season, the bill tip was black as indicated, but the remaining % of the bill, including the orbital skin, was turquoise-cobalt (terminology of Ridgway 1912). Displaying males frequently rubbed the bill over the oil gland during preening with the result that the soft part colors became more intense. As noted by Huxley (1922), the turquoise-cobalt color was typically less intense in females. The entire iris of males was more of a magenta color; in females the inner margin of the iris around the pupil turned to rose. Leg color of both sexes was fleshy maroon.

During the incubation period, the turquoise-cobalt color changed to a mottled yellow in both sexes. The color change occurred first around the eye, then along the rest of the bill. The sexes could then no longer be distinguished. The magenta color of the iris faded, the inner margin around the pupil becoming almost pink in both males and females. The legs became grayish-yellow.

TERRITORY

Louisiana Herons exhibited no pairing behavior outside the breeding season and behaved as solitary individuals while foraging and roosting in the colony. In February a slow 2-fold increase began in the roost population on Grand Island until the heronry swelled to breeding density. Louisiana Herons started to show soft-part breeding color and stayed longer on the island in the morning or returned earlier in the afternoon. Males began spending much time in a certain region of the island that eventually served as their territory. Occasionally a male picked up and manipulated a twig and then dropped it, or tugged on a branch. These actions marked the onset of the breeding season as the males began to set up their territories.

The male set up the territory, often built the foundation of the nest, and undertook the initial defense of the territory from both intruding males and females, as is the case in most North American ardeids (Meanley 1955, Meyerriecks 1960, Palmer 1962). Early male Louisiana Herons staked out large territories with centers far apart; but, as other males began to enter the breeding cycle, the territories gradually became closer and territorial disputes over boundaries became increasingly common. Once a male had selected a site, he preened for long periods. Any disturbance in the vicinity or another Louisiana Heron flying by was viewed intently. Soon after the male had chosen a territory, he began to grasp and tug at branches around the site. A few low intensity performances of the Snap-Stretch display (Rodgers 1977) sometimes occurred between long preening sessions. The male occasionally went below the nest bush and returned with a twig that he used in the foundation of the nest. No matter how long the male displayed, the nest never got past a loosely arranged foundation stage.

Nests generally did not last until the next season so even the earliest males had to construct new foundations when setting up a terriory. However, they often used the stunted and leafless area amidst the branches where a nest existed the previous season. Abandoned nests were almost always used again by a male later in the season. Nest height ranged between 0.3–1.3 m above the high water mark. The early males tended to set up a territory in the dense growth of 1.5–2 m tall mangroves, while the later males nested in the lower, more scattered mangroves.

The initial territory set up by the male Louisiana Heron ranged in size from 4 to 10 m in diameter. Between preening sessions and ever increasing Snap-

Stretch performances, the male roamed his territory, occasionally stopping to preen or display at a site other than the core display site. Initially all herons were threatened upon their approach to the territory and attacked if they did not leave. Pursuit flights were very frequent during this period of the breeding cycle. In general, an intruder was intimidated by the threat display of a resident male and proceeded no further. Once boundaries were established, the territory was recognized and seldom contested; hence aggression between neighboring males decreased with time.

As females were gradually allowed to stay on the territory and an increasing number of new males entered the heronry and began setting up their own territories, the size of the initially large territory gradually shrank. The territory reached its minimum size just after pair formation. This phenomenon is also characteristic of many other ardeids (Meanley 1955, Cottrille and Cottrille 1958, Meyerriecks 1960, 1962). If the nest of the Louisiana Heron was located in one of the low, isolated bushes, the territory sometimes shrank to include only the bush and its immediate vicinity, a diameter of 2–3 m. If the nest was situated in large, dense mangrove, the territory included all the bushtop area above the nest.

Figure 1 shows the history of one region of site A beginning on 11 March 1973, with special reference to male A1. Male A1 displayed from numerous sites, but concentrated display activities on the core mangrove bush. In the late afternoon of 14 March, male A1 paired. From this time on, both male and female participated in the defense of the territory. By 15 June, all nests contained either eggs or young nestlings, with the exception of the abandoned A6 site. Male A6 allowed a female to come onto his nest, where 1 copulation took place. Afterwards, he drove her from the nest and did not allow her back on. Male A6 never paired.

In the large heronry on Grand Island, territory establishment seemed to be staggered. Because the territory of a given pair shrank and left undefended areas, other males moved in and sometimes began displaying as close as 2 m from an incubating heron. These new males were noticeably tense during this period, exhibiting sleeking and constant head turning as they observed the surrounding heronry. With time, they began to roam the mangrove bush, displaying from any site where they would not be threatened or attacked by neighboring herons. Soon a core display site developed, which was usually the place where the nest foundation was begun.

As the courtship period progressed, male Louisiana Herons performed their Snap-Stretch and Circle Flights (Rodgers 1977) from the nest, but often could be observed moving to another site and displaying from there. If the nest or core site was located deep down in the mangrove bush, the male occasionally moved to the bushtop or out on a limb to display, making him

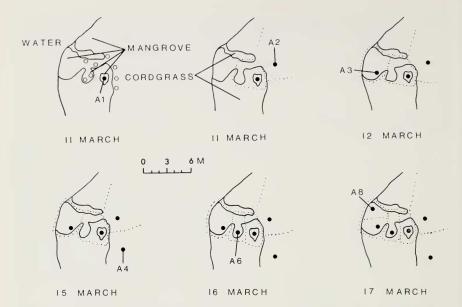


Fig. 1. The history of territory formation in one region of site A during 1973. During the early morning of 11 March, male A1 was alone and displayed from numerous sites designated by open circles, but concentrated display activities on the core mangrove bush designated with a solid circle. Later in the day A2 appeared. Territorial boundaries are indicated by dotted lines and were determined by mapping display sites and the locations of aggressive clashes.

more conspicuous to both roaming females and other territorial males. Territorial male Louisiana Herons oriented the head and looked in the direction of the acoustic cues produced in the Snap-Stretch. After pair formation, the female joined in the defense of the territory, a pattern typical of many other ardeids (Meyerriecks 1960, 1962, Blaker 1969). Later when the nestlings were 3 weeks and older they too defended the nest from both adult and juvenile ardeids when their parents were away.

Certain points should be brought out in regard to the shrinking effect of the male's territory. First, a large territory at the early stage of courtship allowed more display sites and functioned to make the male more conspicuous to females wandering through the heronry. Second, a larger territory had more area from which the female could observe the displaying male without being driven off immediately (Meyerriecks 1960). Third, when the male finally accepted the female and formed a pair bond, a large territory was no longer needed. As a result, more males could come in and occupy newly uncontested areas of the heronry and the high breeding density characteristic of

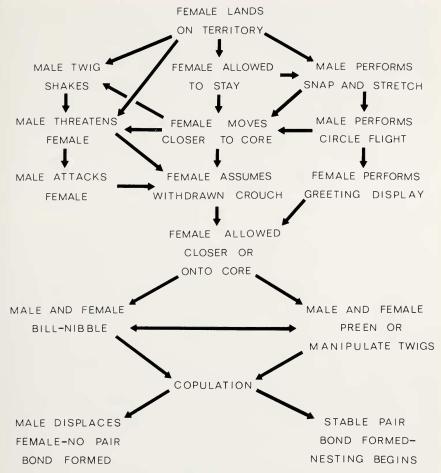


Fig. 2. Possible intercations between male and female Louisiana Herons during the courtship period. For a full discussion see the text.

this species developed. Fourth, the decrease in the territory size permitted the pair to channel their energy away from territory defense and into reproduction. Fifth, because the initial nest foundation served as the core for displaying and later as a site for raising the young, the immediate area around the nest was defended most vigorously at all times.

INTERACTIONS WITHIN THE PAIR

Mate selection.—There are many possible interactions between males and females during the courtship period (Fig. 2). Females at first landed on the

edge of the displaying male's territory. Showing little overt interest in the displaying male or the nest, the females at this time usually did not stop for any great length of time and seemed to be just moving through the colony. If the female moved too far into the territory of the male, he might first exhibit Twig Shaking (Rodgers 1977) or immediately drive her away as he would an intruding male. During the early part of the breeding season females generally did not return when driven away by the male. Later the persistent female would return repeatedly despite repeated threats and attacks by the male. Male Louisiana Herons during the early phase of courtship performed occasional Circle Flights and Snap-Stretches in between long periods of preening or twig manipulation (Fig. 3). The preening exhibited by males during this period was often marked by rapid, forceful, erratic movements. Later, preening movements were more relaxed. With an increase in time, the male performed a greater number of Snap-Stretches (Fig. 3).

At the approach of a female Louisiana Heron, the male generally returned to the core site to perform Snap-Stretch and Circle Flight displays. Once a female became attentive to a displaying male or his nest, she got as close as possible. At first she was thwarted in her attempts to get closer than the edge of the male's territory. Even though performing Snap-Stretches, the male at this time showed predominantly aggressive behavior. Twig Shaking was commonly observed as he threatened the female and often drove her off in pursuit flights. A persistent female was allowed to remain on the edge of the territory, only eliciting mild feather erection in the male. Continual attempts by the female eventually resulted in her getting within a short distance of the nest. During this time, the male repeatedly did Twig Shakes. He threatened the female with Upright and Forward displays (Rodgers 1977) and occasionally drove her back some distance or even off the territory. Often the female remained in view after being chased off by the male and returned onto his territory repeatedly, especially during the late stages of the courtship phase. Meyerriecks (1960) described similar behavior on the part of the female Green Heron (Butorides virescens).

The presence of a female initially increased the frequency of Snap-Stretch and Circle Flight displays, which were occasionally performed in rapid succession (Fig. 3). The maximum number of displays observed during any 1 min ($N=8328~{\rm min}$) was 5 Snap-Stretches and 3 isolated Snaps performed by male A1 with a female on the territory.

The female intently observed the male displaying, preening, and arranging twigs in the nest. Her attention seemed to be directed not only to the male, but the nest foundation if present. When the male performed the Circle Flight, the female watched the entire performance. Females were often observed jumping onto the nest while the male was engaged in the Circle Flight. Upon

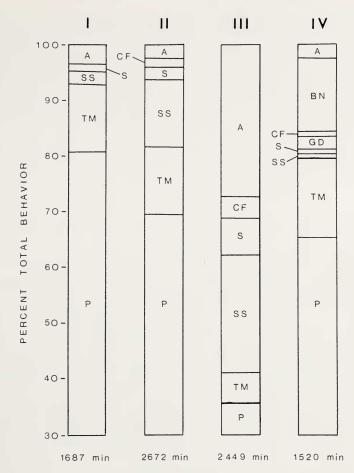


Fig. 3. Shifts in the behavioral repertoire of male Louisiana Herons. Phases of the courtship period are: I, first ½ h of displaying; II, after first ½ h of displaying; III, behavior with a female present; IV, last ½ h before copulation. Abbreviations are: A, aggressive behavior (includes the Upright, Forward, and Twig Shake displays); BN, Bill-nibble; CF, Circle Flight; GD, Greeting display; P, preening; S, Snap; SS, Snap-Stretch; TM, twig manipulation.

his return, the male always attacked the female and drove her away. Occasionally, as many as 3 females joined the male in the Circle Flight by flying after him and landing nearby when he returned to his nest. The female's flight did not in any way resemble the initial components of the Circle Flight of the male, but the return flight was similar in posture and calls to the Greeting display phase performed by the male (see Rodgers 1977).

The female was allowed closer and closer until she was within 1–1.5 m of the nest. She attempted to get even closer and assumed the Withdrawn Crouch (Rodgers 1977). During an encounter with a threatening or attacking male, female Louisiana Herons often performed elements of the Greeting display, which appeared to function in reducing the aggressiveness of the male (Rodgers 1977). Often the male stopped his attack and temporarily joined in the performance of the Greeting display. This outcome allowed the female to hold her position or move slightly closer to the nest.

As the female assumed the Withdrawn Crouch, she frequently Bill-nibbled (Rodgers 1977). If she rose from her low-profile posture, she was attacked and driven off. When the female was on or near the edge of the nest, the male exhibited a tendency toward a reduction of Snap-Stretch and Circle Flight displaying (Fig. 3). In addition, much preening and Bill-nibbling was done by the female, with a slow increase in the frequency of Bill-nibbling by the male (Fig. 3).

Precopulatory period.—This period of courtship from the time the female is first tolerated on the nest to just before the first copulation by the potential pair was marked by a switch from aggressive to sexual behavior in the male. For long periods both male and female engaged in preening, interrupted by twig manipulation and Bill-nibbling. This appears to be typical of precopulatory behavior of most ardeids (Meanley 1955, Cottrille and Cottrille 1958, Meyerriecks 1960, 1962, Blaker 1969). The male Louisiana Heron still exhibited moderate feather erection, while at the same time Bill-nibbling became more frequent. He rarely performed the Snap-Stretch and Circle Flight displays once the female was on the nest (Fig. 3). The 2 herons often stood side by side, usually facing in opposite directions for periods up to 40 min. The female then rose out of the Withdrawn Crouch and stood with the male in the center of the nest without being attacked.

Copulation.—Soon after the female succeeded in getting onto the nest, the pair copulated either on (36 of 39 observations) or close to the nest platform or core display site. The male watched the female as she began manipulating twigs in the nest, and they both often Bill-nibbled. The female leaned forward, withdrew the head partially, and squatted. This act probably indicated to the male that she was ready to copulate. I observed no precopulatory display. The male mounted the female from the rear or the side by stepping up onto her back. Flapping his wings to maintain his balance, he squatted on her, grasping her shoulders with his toes. He also used leverage of his bill on the shoulder and neck region of the female for additional support. Meanley (1955) reported similar use of the bill by the male Little Blue Heron (Florida caerulea). Copulations ranged in duration from 8 to 11 sec (mean 9.8 sec; N=23). No feather erection, nor any calls were noticed at any time preced-

ing, during, or immediately after copulation. Finishing copulation, the male rose and stepped off the back of the female. Copulation seemed to occur irregularly during the early phase of pair formation, though I observed copulations throughout the egg-laying period.

The length of time a male maintained a territory and engaged in courtship behavior without pairing is not accurately known. One instance recorded was the occupation of a territory by male A6 for only 4 days before abandoning it. Male A11 maintained a territory for 11 days before pairing.

Although I did not mark adult Louisiana Herons. I believe they practice seasonal monogamy. In 2 years, I observed no evidence of promiscuity once the male and female had paired, nor "rapes" as have been reported for the Little Blue Heron (Meanley 1955).

Postcopulatory period.—Immediately after the first copulation, the pair members engaged in long periods of preening, Bill-nibbling, and manipulating nest twigs. They also spent a lot of time standing side by side, facing in opposite directions. In this position, Huxley (in Bent 1926) has said they "intertwine their necks," but this is actually an illusion produced by their relative positions. The female soon began rearranging the twigs in the nest with the male looking on. Occasionally, both herons suddenly engaged in short performances of the Greeting display.

If the female left the nest after the first copulation to preen or find twigs, the male might not allow her back onto the nest. I observed 4 instances (N = 39 copulations) in which a male copulated with a female and then attacked her and drove her off or did not allow her return onto the nest after she had left it momentarily. This led to dissolution of the bond in 2 instances when the male repeatedly repulsed the female's attempts to get back on the nest.

Males under observation did not feed while courting. The presence of wandering females and intruding males may be the reason for their abstinence. Only after pair formation, with the presence of its mate to defend the territory, could the male forage without danger of losing his territory. Jenni (1969) also reported that male Louisiana Herons do not feed during the courtship period.

NEST BUILDING

The male was usually the one who went out and found twigs. Male Louisiana Herons passed these twigs to the female, who then worked them into the nest. Typically the period from the first copulation to the initiation of stick collecting was short. For example, pair A9 copulated at 11:43 and the male returned with the first twig in 11 min. Most twigs were gathered from on or very near the territory, but occasionally males brought material from greater distances. Birds would also take twigs from abandoned nests nearby.

When the male returned with a twig in his bill, the pair performed the

Greeting display (Rodgers 1977). Reaching out, the female took the twig in her bill and both engaged in additional head nodding and calling. The female then placed the twig in the nest as the male looked on. The male often Bill-nibbled while the female was inserting the twig. Initially, the male exhibited considerable feather erection while passing twigs to his new mate. This feather erection decreased as nest building continued and was limited to the crest and, to a lesser extent, the aigrettes.

The nest foundation begun by the male during the courtship period consisted of large twigs about 1 cm in diameter and 30–60 cm long (N=27). This structure sometimes had only 2 or 3 twigs. Twigs brought to the female after pair formation, while occasionally large, usually were about 0.5 cm in diameter and shorter than 30 cm (N=163). The finishing material consisted of small, flexible twigs and *Spartina* grass stems. The completed nest varied in width and depth, but always had a slight depression on the top surface that prevented the eggs from rolling out. I could distinguish no differences between the nests of Louisiana Herons and those of Little Blue Herons or Snowy Egrets (*Egretta thula*) on Grand Island.

During nest building, one member of the pair was always on or near the territory. This prevented neighboring herons from stealing nest material. After the nest was completed, both sexes occasionally added twigs to the structure for repairs between periods of incubating or brooding. The interval between the first copulation and the laying of the first egg for 2 pairs of Louisiana Herons on Grand Island was 4 and 6 days. Jenni (1969) recorded periods of 4 and 5 days at Lake Alice, Florida.

INCUBATION STAGE

During the interval before the eggs were laid, the female spent a great amount of time squatting down on the nest, rearranging the nest twigs, and placing in new material. On Grand Island, the clutch size averaged 3.0 eggs (range = 2-5, mode = 3). Of the 99 nests examined, 22 contained two eggs, 58 three eggs, 18 four eggs, and 1 had five eggs. For Lake Alice, Jenni (1969) recorded the average clutch size for 35 nests as 4.1 eggs (range = 3-9, mode = 4). Teal (1965) reported an average of 3.1 eggs per clutch for 15 nests (range = 2-4, mode = 3) for Sapelo Island, Georgia.

After the clutch was completed, the pair was usually together only during a nest relief. Both sexes incubated. Nest reliefs were irregular and were accompanied by the Greeting display and Bill-nibbling. The returned heron usually preened or manipulated a few twigs in the nest before settling. Its mate often preened a short time on the edge of the nest before leaving to collect I or more twigs which were passed in a Greeting display to its mate who inserted them into the nest. Huxley (in Bent 1926) stated the number may be

as many as 11 twig presentations at 1 nest relief. My data indicate 2-5 presentations (mean 4.2, N=167) are more common. Because the nests are in good condition structurally, I believe the display functions to reinforce the pair bond in these instances. Sometimes an incubating heron did not immediately rise off the nest when its mate returned, but remained sitting on the eggs. The returned heron then engagd in additional Greeting displaying and Bill-nibbling, after which the mate would rise off the nest.

The length of an incubation period varied considerably, from periods of less than 1 h to 1 recorded instance in which the partner did not come back during the daylight hours (about 06:00 to 20:30). Such long periods between changeovers were rare, and although nest reliefs were irregular, there tended to be 1 during the mid-morning, another during the mid-afternoon, and often 1 during the early evening. Incubation was most continuous in the early morning and early evening periods, when the ambient temperatures were cooler. During these periods the adult only occasionally rose off the eggs to preen, rearrange nest material, or sunbathe. During the late morning and afternoon, when the temperatures were the warmest, the Louisiana Heron often rose off the eggs. The bird rarely left the eggs unattended: usually it stood on the nest edge while preening or sunbathing. I never saw an incubating bird leave the nest to forage in nearby shallow inland pools. As the heron sat again on the eggs, it first erected the feathers of the lower breast and belly, then dropped the wings slightly, and shifted from side to side as it lowered its body onto the eggs. Mild crest erection also occurred.

Incubating Louisiana Herons were quick to rise and threaten any species of heron intruding on the territory. The area immediately around the nest was defended most vigorously. Disturbances outside the territory usually elicited only the Alert Posture (Rodgers 1977).

At pipping, the young Louisiana Heron emits high-pitched "peeping" sounds. During this time, adults looked at the eggs for long periods of time, sat, then rose again and peered at the eggs while turning the head from side to side. The adult heron later dropped pieces of eggshell out of the nest.

BROODING AND CARE OF THE YOUNG

Because incubation begins with the first egg, hatching is asynchronous. Until the nestlings were about 1 week old, the behavior of the adults was the same as during the incubation period, except for feeding the young. Adults brooded most intensively during the cool periods of morning and early evening. Herons commonly sunbathed while squatting on the nest or standing over and shading the nestlings.

From age 1 day to about 1 week, nestlings were fed small fish that were regurgitated by the parent onto the floor of the nest. The nestlings picked

up the fish in their bills. Similar behavior has been reported for the Little Blue Heron (Meanley 1955), Great Blue Heron, Ardea herodias (Pratt 1970), and Cattle Egret Bulbulcus ibis (Weber 1975). Afterwards the adult ate the unconsumed fish. Upon nest relief, the departing parent often fed the nestlings 1 more time.

When the young were 1–2 weeks of age, the bill, legs, and general body strength were well enough developed to allow grasping of the parent's bill and they obtained a meal directly from the adult. The young were then fed one at a time with the adult leaning forward and extending the mandibles downward in such a manner that the dorsal surface of the upper mandible faced the offspring and was grasped. After feeding one nestling, the adult usually moved a short distance from the calling chicks before returning and feeding a second. This process was usually repeated several times. In such sessions, 1 nestling was often fed twice. Adults stood on the edge of the nest and could easily elude clamoring 1–2-week-old chicks: older young chased the parent around the nest bush. Hence, between feeding bouts the adult flew a short distance away to rest, preen, or sunbathe.

After the nestlings were 3-4 weeks old, the parents were seldom seen with the young except when feeding them. Pratt (1970) reported parent Great Blue Herons stay away after the young are 28 days old: Weber (1975) found that 14-21-day-old Cattle Egret chicks are left by themselves. Perhaps as the young Louisiana Herons got older, almost constant effort on the part of both parents was required to supply the developing juveniles with an adequate quantity of fish. Siegfried (1972) found that Cattle Egret nestling growth curves are steepest (hence high food demands), and chick mortality due to starving is highest at the time when both parents switched from alternate to simultaneous hunting regimes. Also, young Louisiana Herons at this age were old enough to defend themselves. With 4-5-week-old juveniles, the parent did not land on its nest bush but landed 2-5 m away, gave a series of "scaah" calls and waited for its offspring to come to it. During this time, the parent exhibited moderate feather erection which increased slightly as the young approached to receive food. As food was transferred directly to the juvenile, both the parent and young herons rapidly flapped their wings to maintain an upright position. After feeding its brood, the parent stepped and faced away, then reswallowed any fish that remained in its mouth.

Because parent Louisiana Herons refused to feed many begging juveniles that approached them, I suspect that they were able to recognize their young. Generally, the young 3–4 weeks old were the ones that approached nonparents for food. The older juveniles apparently learned to recognize their parents and probably by the process of habituation (in the terminology of Thorpe 1963), they learned that they would not get food from but would be at-

tacked by a nonparent heron. Skead (1966) noticed adult-young recognition in the Cattle Egret.

The parents returned at irregular times to feed their young. The number of feedings was usually 4 or 5 per day. When the juveniles were 7–8 weeks old, the parent-young bond had disintegrated and the juvenile herons were on their own. The adult pair bond dissolved at the same time as the parent-young relationship. The parents were no longer observed together at the nest, which by this time had disintegrated and fallen through the mangrove.

Commonly 1 nestling (less often 2) died in the nest. These were generally the youngest and therefore the smallest. Because they were at a physical disadvantage in competing with older, more aggressive siblings for the limited amount of food, they became emaciated and starved to death. On Grand Island during 1973, I recorded a mortality rate from egg laying to the 2-weekold age of 22.5%. Of the 34 nests, 1 contained one nestling, 15 two nestlings, 17 three nestlings, and 1 had four nestlings. Jenni (1969) calculated a mortality rate of 35.8% for 28 nests for the same nestling period. Teal (1965) reported a mortality rate of 68% from egg laying until the young were fledged. I attribute most of the nestling mortality on Grand Island to starvation of the younger nestlings. I saw no evidence of predation by raccoons (Procyon lotor); Boat-tailed Grackles (Quiscalus major) destroyed some eggs in a small region of the heronry outside my study area. Nestlings occasionally died after becoming entangled in mangrove branches during wind storms or while wandering from the nest. A factor that may have contributed to the low mortality rate on Grand Island is that the Barataria Bay estuarine marsh is rich faunistically and provides a good nutrient source throughout the breeding season (Day et al. 1973).

SUMMARY

Observations on the breeding behavior of the Louisiana Heron were made in a large heronry on Grand Island, Barataria Bay, Plaquemines Parish, Louisiana. Male Louisiana Herons with breeding soft-part colors set up large territories initially. The male appeared tense at first but soon began performing Snap-Stretch and Circle Flight displays. Soon after establishing a core display site, a male constructed the foundation of the nest there. During the early courtship period the male defended his territory from both intruding males and females. As additional males entered the breeding cycle and females began to move through the heronry, the size of the male's territory shrank.

At first a male threatened and chased away all females, but a persistent female was soon tolerated on the edge of the territory. The frequency of Snap-Stretch and Circle Flight displays increased with time and in the presence of the female. With time, she was allowed closer and closer to the nest. Assuming the Withdrawn Crouch, the female was finally allowed onto the nest where copulation took place within a short time. Later the female was allowed to occupy the center of the nest and began final construction.

The male brought twigs to the female on the nest as both engaged in the Greeting display and Bill-nibbling.

The first eggs appeared 4-6 days after the initial copulation. On Grand Island the average clutch size was 3.0 (range \pm 2-5, mode \pm 3, N \pm 99). Both sexes incubated. When one mate returned, the pair engaged in the Greeting display before the heron that was relieved flew off.

Both sexes fed the young, at first regurgitating small fish onto the floor of the nest. Nestlings 2 weeks and older fed by grasping the bill of the parent. Adults brought food to the brood 4-5 times a day. Many of the youngest nestlings died of starvation; chicks of all ages occasionally died in accidents. A mortality rate of 22.4% was recorded for nestlings on Grand Island for the period from egg laying through the second week after hatching. The parent-young bond began to break down when the juveniles were 6-7 weeks old.

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